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Review

Advances in Microclimate Ecology Arising from Remote Sensing

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Microclimates at the land–air interface affect the physiological functioning of organisms which, in turn, influences the structure, composition, and functioning of ecosystems. We review how remote sensing technologies that deliver detailed data about the structure and thermal composition of environments are improving the assessment of microclimate over space and time. Mapping landscape-level heterogeneity of microclimate advances our ability to study how organisms respond to climate variation, which has important implications for understanding climate-change impacts on biodiversity and ecosystems. Interpolating *in situ* microclimate measurements and downscaling macroclimate provides an organism-centered perspective for studying climate–species interactions and species distribution dynamics. We envisage that mapping of microclimate will soon become commonplace, enabling more reliable predictions of species and ecosystem responses to global change.

Highlights

Microclimates are often neglected in ecology and evolution, despite mounting evidence that microclimates matter for ecosystem dynamics and processes, such as the response of organisms to climate change.

Remote sensing approaches to measure the 3D structure and thermal composition of terrestrial ecosystems significantly advance microclimate modeling and mapping. This provides novel opportunities for fundamental and applied microclimate ecology, forestry, and agriculture.

Increased efforts to use remote sensing to upscale *in situ* microclimatic measurements will further our mechanistic understanding of how topography and vegetation structure determine microclimate.

Detailed spatial and temporal microclimate data derived from remote sensing may lead to more realistic predictions of microclimate and the associated biotic responses to global change.

Importance of Microclimate Maps

Local modification of the **climate** (see Glossary) by topography and vegetation produces **microclimates** at the land–air interface which can differ greatly from the climatic means [1,2]. Surface temperatures between north- and south-facing mountainsides, for example, can vary by 20°C, equivalent to a latitudinal gradient of about 2000 km [3]. In addition, forest canopies can buffer the diurnal amplitude of air temperature in the forest **understorey** by 7°C [4]. Such differences in temperature within landscapes matter to organisms, affecting processes such as respiration as well as heat and energy exchange which, in turn, set thermodynamic constraints on species behavior, growth, reproduction, and survival [5–7]. Innumerable papers over the past century have quantified microclimates and their influences on ecological processes at all levels of organization, from physiological processes of single organisms to ecosystem-level productivity and nutrient cycling [4–6,8–10]. Microclimate is also relevant to evolution because phenotypic and genotypic adaptations are driven by environmental conditions actually experienced by the organisms [11]. Moreover, microclimate mapping and monitoring have been recognized as key to effective natural resource management, with forestry, agroforestry, and agriculture being prominent examples [6,12].

Microclimate ecology is attracting renewed attention owing to its fundamental importance in understanding how organisms respond to climate change [2]. Species distributions are typically modeled using **macroclimate** data obtained from national networks of weather stations [13,14]. These standard meteorological data are measured in open areas at 1.5–2 m height above short grass, and capture synoptic conditions that are unrepresentative of the range of microclimates that most organisms experience [15,16]. These inaccuracies and biases can have serious implications when predicting organismal responses to climate change. For example, recent studies suggest that many plant and animal communities are accumulating

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a **climatic debt** because they are migrating more slowly than necessary to keep up with macroclimate warming [17–22]. However, **temperature buffering** near the ground – owing to local radiation regimes, soil characteristics, and topography – means that organisms may not need to migrate, or adapt, as quickly as previously thought to keep pace with the shifting macroclimate [23,24] (Box 1). Thus, extinction risk from climate change for plants and insects is considerably reduced by the occurrence of **microrefugia** within landscapes with highly heterogeneous microclimates [25]. Nevertheless, the modulating effects of microclimate variability on climate change impacts have only recently started to be quantified [3,21,25–29].

A key impediment to progress in incorporating microclimate into models of how climate change impacts on organisms has been our limited ability to map and monitor microclimatic variation over large spatial scales and over time. Networks of microclimate sensors provide point-based measurements and weather stations provide macroclimate data, but we have lacked approaches to effectively interpolate and downscale this information. **Remote sensing** is now offering opportunities to lift this technical barrier by producing detailed and spatially continuous data-layers that can be used as explanatory variables to understand and model the horizontal and vertical variation in microclimatic conditions over large spatial and temporal scales. We review here how these emerging technologies are advancing microclimate modeling and mapping, and highlight some of the opportunities they provide for ecology, conservation, and climate change research.

Eureka: Remote Sensing Advances for Modeling and Mapping Microclimate

Remote sensing technologies are increasingly capable of mapping the structural complexity and thermal composition at the ground–atmosphere boundary at scales relevant to studying

Box 1. Shifts in Species Distributions in Response to Global Warming

Microclimate – the local modulation of macroclimate by vegetation canopies and topographic position – affects species redistribution under climate change (Figure I). Maps of microclimate predicted from remote sensing data can improve habitat suitability maps and predictions of how species will respond to climate change.

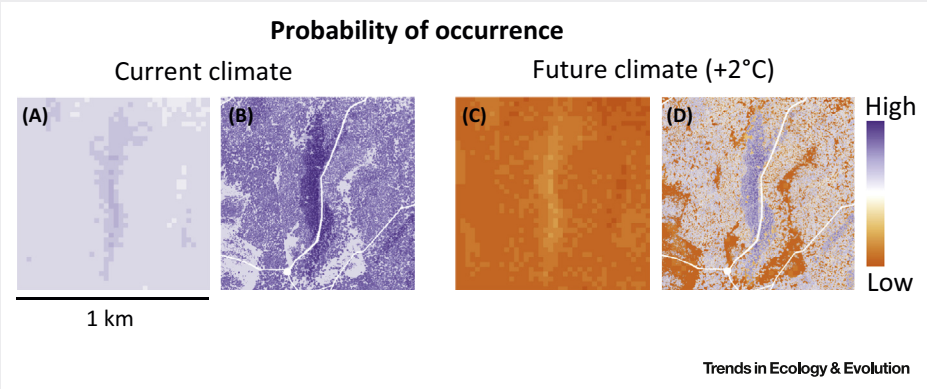

Figure I. Probability of Occurrence maps Based on a Virtual Species Approach. The realized niche of the species is known and predicted with current-day macroclimate (A), microclimate (B), and projected into the future under a 2°C warming scenario (panels C and D, respectively). The temperature data for images (A) and (C) refer to long-term (30 year averages during the period 1970–2000) maximum temperature of the warmest month, and were obtained by downscaling macroclimate at 25 m resolution to incorporate topoclimatic processes. Spatial variation in microclimate (temperature in this case) generated by trees (i.e., canopy cover) and topography (i.e., topographic concavity) was modeled using 50 cm resolution maps (B,D) derived from 3D airborne LiDAR. Note that microclimatic models indicate much larger areas of suitable habitat than do macroclimatic models. In particular, many potential microrefugia are identified in (D) which could continue to provide suitable habitat under climate warming. Figure adapted, with permission, from Lenoir *et al*. [24].

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organismal responses to environmental variation [27]. We discuss the contributions that laser scanning, photogrammetry, hyperspectral imaging, and **thermal imaging** are making.

Airborne Light Detection and Ranging (LiDAR) (also known as airborne laser scanning) is particularly valuable for modeling and mapping microclimates because it provides spatially continuous, sub-metre-scale information on two key modifiers of climate at the ground–atmosphere interface: ground topography and vegetation structure [30]. To construct maps, microclimate measurements taken on the ground using sensor networks are related to LiDAR structural information, such as topographic position and light incidence at very high resolutions (Boxes 2–4), using statistical modeling approaches, and the function generated by this approach is then used to predict microclimates across the entire LiDAR-mapped landscape (Figure 1) [13,31–35]. Effective interpolation requires that the sensor networks sample contrasting sites within the study area. The sensor data must also be summarized in ecologically meaningful ways, guided by clear research questions [36]. For example, the frequency of extremely cold or hot temperatures, calculated over timescales relevant for the growth and survival of organisms, are more meaningful for biogeographic applications than are average conditions [2,36].

Aerial photography provides an alternative approach to assessing topography and forest structure by using photogrammetry and structure-from-motion (SfM) techniques to construct 3D surfaces (Figure 2) [37]. These inexpensive and easy-to-use methods are increasingly applied, but are less accurate than LiDAR at deriving terrain elevation beneath tree canopies, or for measuring vertical vegetation structure, because photographs only record reflectance off the upper surface [38,39]. One-off mapping of large areas using LiDAR and aerial photography is normally conducted from manned aircraft, while unmanned aerial vehicles (UAVs, e.g., drones) equipped with miniaturized cameras and LiDAR sensors are becoming available to map smaller areas at even higher spatiotemporal resolution. Using UAVs and SfM techniques, Milling *et al*. [40] found that summer maximum temperatures may vary by up to 4°C over only a few meters within sagebrush–steppe landscapes – habitats that were previously considered to be relatively homogeneous. A key advantage of UAVs is that deployment is very flexible, enabling the collection of time-series of aerial imagery over a period of interest at relatively low cost. SfM techniques applied to image time-series offer novel opportunities for monitoring microclimates in ecosystems in which phenology creates strong temporal variation in microclimate [41,42].

Terrestrial laser scanning (TLS) provides immensely detailed datasets of vegetation structure that can be used to model microclimate. Complementary to airborne laser scanning, which

Box 2. Measuring How Plant Canopies Affect Solar Radiation Fluxes

Solar radiation flux has strong effects on the energy budget and performance of organisms living beneath vegetation canopies. Radiation regimes along the vertical canopy profile of forests can be estimated from a LiDAR point cloud by creating a 3D map of foliage presence/absence in voxels (i.e., 3D pixels) and then apply ray-tracing algorithms to evaluate whether beams entering the canopy at different locations and angles are likely to be intercepted [31,87]. Alternatively, LiDAR data can be used to generate synthetic hemispherical images from which fluxes of non-directional diffuse sky radiation and direct solar radiation, or light extinction following the Beer–Lambert law [88], can be calculated for any time in the day or year (Figure I). These approaches are computationally intensive but better represent light conditions experienced by forest organisms than do simple approaches based on canopy cover [89]. Vegetation structure thus drives the interception of solar radiation, which means that the importance of vegetation structure for microclimate will vary between day and night and in different weather conditions, with the temperature offsets being highest on bright sunny days. Advances in physically based radiative transfer modeling now make it possible to estimate the 3D radiative budget in forests and open lands at an ever-increasing detail, for example by accounting for foliage-specific filtering of different wavelengths [90].

Glossary

Airborne light detection and ranging (LiDAR): a remote sensing technology used for 3D analysis of Earth surface environments (also known as laser scanning). A LiDAR sensor emits about 200 000 laser pulses per second towards the ground and measures the energy waveform returning from backscattering objects. When used to measure vegetation structure, the light pulse is wider than a typical leaf by the time it reaches the upper canopy, meaning that some of its energy passes through the upper canopy to lower layers and even the ground. The sensor converts the continuous waveform of returning energy into 'discreet returns' and, by precisely recording return times and its location in the air, creates a 3D point cloud of the position of objects. The point cloud is used to derive high-resolution of topography and canopy height (see DTM and CHM) and detailed information on vertical vegetation structure that is spatially continuous across large areas. Some LiDAR sensors record the full waveform, providing detailed information about the entire vertical forest profile. The added value of full-waveform over discrete LiDAR for microclimate mapping remains to be tested.

Alpha diversity: species diversity in sites or habitats at the local scale (e.g., point-based surveys), often expressed as the total number of species (species richness) or abundance weighted indices such as the Shannon index and the Simpson index.

Beta diversity: a diversity measure expressing variation (turnover and nestedness) in community composition among habitat gradients; can be calculated based on taxonomic (e.g., species identities), functional (e.g., functional traits), and phylogenetic (e.g., branches) units.

Canopy height model (CHM): a continuous digital surface – usually in the form of a raster dataset – that represents the height of the canopy above the underlying terrain.

Climate: synthesis of atmospheric conditions characteristic of a particular place in the long-term (usually 30 year averages) expressed

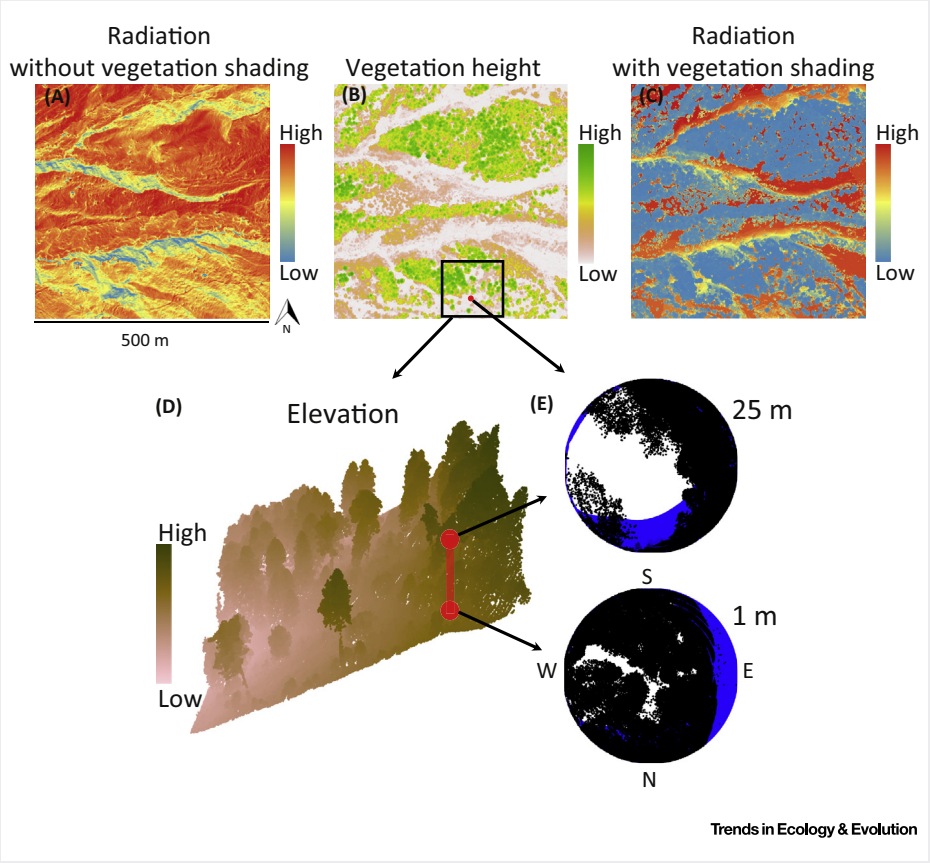

Figure I. Using Airborne LiDAR To Map Solar Radiation Fluxes in a Mountainous Region. (A) Potential clear-sky solar radiation predicted to reach the ground on a summer day if vegetation is absent (i.e., based on a digital terrain model generated by LiDAR). (B) Forest canopy height measured over the same region. (C) Potential clear-sky solar radiation calculated to reach the ground having penetrated through the forest canopy, assuming increased shading with increasing vegetation cover and height. It can be seen that much of the landscape is deeply shaded by trees and shrubs, making it suitable for shade-tolerant plant species. (D) 3D airborne LiDAR-derived elevation data of a forest (black rectangle in B) are used to construct synthetic hemispherical images at 1 m and 25 m height above the forest floor [85]. (E) Reconstructed hemispherical images, taken at the red point position in (B), show portions of the sky obscured by trees (black) and the terrain (blue), from which diffuse and direct light transmission can be calculated. These images can be calculated for any point in the landscape and at any height in forest canopies, providing unprecedented opportunities to estimate the microclimate in the neighborhood of individual organisms. Note that the ground topography (elevation, aspect, and slope) has a strong influence on solar radiation [86], and high-resolution DTMs from LiDAR surveys provide crucial input data for quantifying these effects [13,14].

maps 3D vegetation structure from above, TLS maps vegetation in extraordinary detail from below, thus providing information on the understorey structure. Kong *et al*. [43] found that TLS-based reconstructions of canopy volumes coupled with microclimate measurements revealed cooling effects in the understorey that varied among tree species, suggesting that TLS can pick up subtle effects of different leaf sizes on understorey microclimate. Moreover, Ehbrecht *et al*. [44] found that TLS-derived measurements of canopy openness were positively related to diurnal temperature ranges in managed temperate forests in Germany. TLS measurements are restricted to a few hectares and are of limited use, compared to airborne laser scanning, for modeling microclimate over large areas. Nevertheless, the forest understorey-structure

by averages of various elements of weather and probability distributions of extreme events.

Climate debt: biotic responses observed in nature are often slower than expected under the assumption of complete synchrony with climate change; climate debt describes the spatiotemporal lag accumulated by a species or a community compared to the actual shift in climate.

Cold air drainage: gravity-induced, downslope flow of relatively cold air near the ground, pooling in local depressions and valley constrictions. A prominent phenomenon in mountain valleys at night and during winter.

Digital terrain model (DTM): a continuous digital surface representing the elevation height of the bare earth. Sometimes also referred to as a digital elevation model (DEM).

Hyperspectral remote sensing: image analysis based on the spectral reflectance across a wide range of the electromagnetic spectrum; also known as hyperspectral imaging or imaging spectroscopy.

Macroclimate: climate conditions above ground or above the canopy (e.g., >2 m) at a relatively large scale, for example across spatial dimensions of 1 km or more, and with temporal dimensions of days to weeks or longer.

Microclimate: climate conditions close to the ground (e.g., <2 m) or along vertical forest profiles at relatively fine spatiotemporal resolutions, for example across spatial dimensions of centimeters to meters, with temporal dimensions of minutes or shorter. Microclimate conditions include temperature, precipitation, humidity, wind, and radiation regimes.

Microrefugia: spatially restricted local habitats that sustain a climate that has become, or is becoming, lost owing to climate change and that enable species to persist in an otherwise inhospitable region.

Remote sensing: acquiring information about an object or phenomenon from a distance.

Temperature buffering: below a plant, especially forest canopies, daily air temperatures may be substantially buffered, increasing less during the day and decreasing less

information that TLS provides at the plot level has been shown to improve landscape-level vertical vegetation structure mapping based on full-waveform airborne LiDAR [45].

Complementing maps of 3D vegetation structure, maps of leaf functional traits and species obtained by **hyperspectral remote sensing** [46,47] are likely to improve the statistical fit of microclimate models. We expect this improvement because the quality and quantity of solar radiation transmitted by canopies vary according to leaf traits and tree species, leading to species-specific microclimatic conditions in the understorey [48]. However, we are unaware of studies using hyperspectral remote sensing to map microclimate (see Outstanding Questions).

Thermal imaging using thermal infrared (TIR) cameras can be applied to map surface temperatures. As opposed to LiDAR technologies, TIR cameras directly record long-wave infrared radiation (i.e., 7.5–14 μm) emitted by an object or organism, which is linked to surface temperature according to Boltzmann's law when surfaces have high emissivity [3,49]. The surface and body temperature of an organism is related to its energy budget and thus to the functioning and performance of plants and animals [7,50]. Nonetheless, the surface temperature is not necessarily related to the air temperature an organism experiences. For instance, plants respond to water shortage by closing stomata and reducing transpiration, which causes leaf surface temperatures to rise; irrigated and non-irrigated plants can differ in leaf temperature by several degrees but have similar air temperature in their surrounds, as measured with shielded temperature sensors (Figure 2). TIR images recorded by UAVs have centimeter resolution [49], providing valuable means for fine-scale monitoring and management of water use and water stress by plants, for example in crop production [51,52], or to assess the temperature experienced by insects living on leaf surfaces. However, TIR images might not necessarily reflect atmospheric or soil microclimatic temperatures experienced by plants, in other words their thermal niche.

during the night than outside the forest canopies.

Terrestrial laser scanning (TLS): the process of gathering 3D data using a LiDAR instrument on the ground. 3D point clouds produced by TLS are typically much denser than those obtained by airborne LiDAR.

Thermal imaging: technique to produce an image based on the heat emitted by an object or an organism.

Understorey: a layer of vegetation close to the floor beneath the main canopy of a forest.

Vapor pressure deficit (VPD): the difference between saturation vapor pressure and the actual vapor pressure at a given temperature.

Box 3. Temperature Buffering and Offset

Solar radiation reaching the land–atmosphere interface is mostly reflected, or absorbed and re-emitted as thermal radiation, or drives evapotranspiration. Vegetation canopies lift energy-exchange surfaces off the ground, and in doing so modulate radiant fluxes, air temperature, and humidity at ground level. The capacity of plant canopies to sustain a different temperature below the canopy compared to free-air conditions (i.e., a temperature offset) is thus closely related to canopy structure and composition. Under the canopy, diurnal changes in temperatures are less extreme than above the canopy, and this temperature buffering is modulated by canopy height and cover, both of which can now be precisely mapped [13,32,91].

Sensor networks sampling environmental gradients (*cf.* Figure 1 in main text) are increasingly combined with remote sensing data to map microclimate. The current scientific literature often makes crude assumptions about the shading and temperature-buffering effect of vegetation when modeling microclimate, and usually neglects systematic changes in the temperature offset over time, in other words the offset trend (Figure I) [24,28]. The degree to which temperatures below the canopy are offset compared to free-air conditions will not be constant over time and depends on successional processes driving dynamics in canopy structure and composition. Long time-series of below-canopy temperature records thus need to be related to forest dynamics to better understand the drivers of long-term microclimatic dynamics [24]. Such data are rarely available [92], and global long-term networks such as FLUXNET may prove very valuable in this respect.

Forest microclimates are also affected by landscape features such as distances to forest edges, urban areas, and large water bodies. Many of these landscape features can be retrieved from remote sensing data [4,29,32,35,93] and integrated into predictive models used to map microclimate. Another key influence on spatiotemporal dynamics in microclimate is topographic position because it determines the influences of cold air drainage and pooling on a site [94,95]. Topographic position and cold air drainage can be estimated from high-resolution digital terrain models (DTMs), further increasing our ability to map and model microclimate across broad spatial and temporal scales.

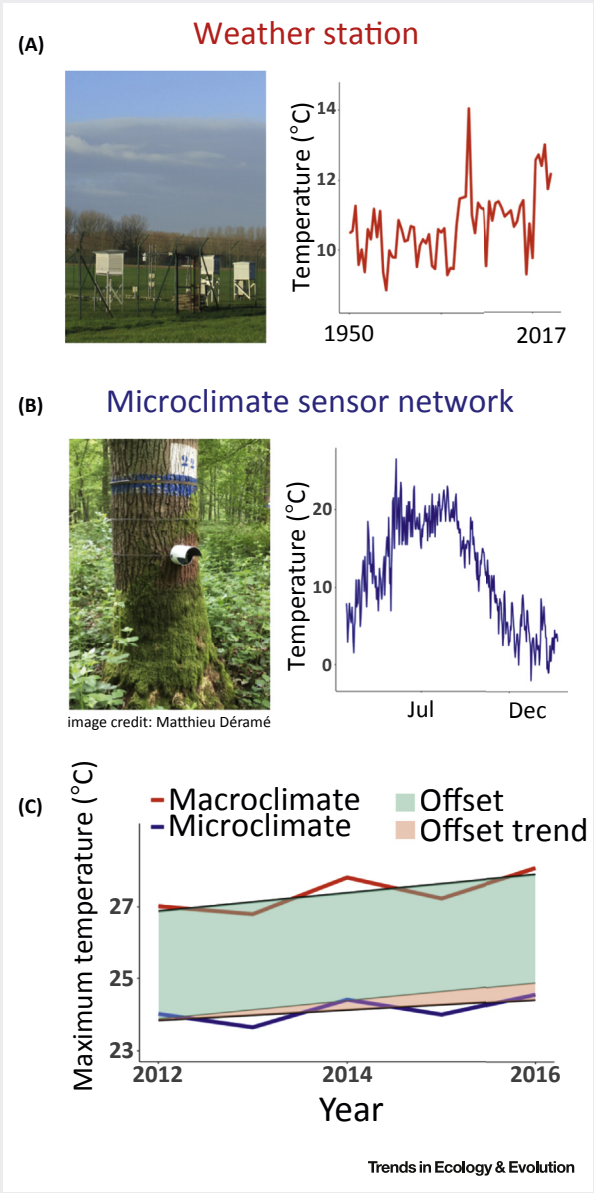

Figure I. Microclimate Dynamics may Deviate from the Macroclimate. (A) Weather stations as illustrated on the left provide long-term climate data for synoptic conditions (right panel). (B) Microclimate data from sensor networks *(cf* Figure 1 in main text) are currently available mostly for short time-periods only, for example months to a few years (right panel). The left image shows a shielded sensor placed on the north side of a tree trunk. (C) Maximum air temperatures below canopies (i.e., microclimate) are frequently offset by several degrees compared to free-air conditions (i.e., macroclimate), and the offset trend over time may vary. Long-term data series are necessary to assess the differences in spatiotemporal dynamics between macro- and microclimate (see text).

Surface temperatures from high-resolution TIR images have been applied for fire and disease detection, phenotyping in plant breeding, wildlife monitoring, and microclimate ecology (reviewed in [42,52]). Senior *et al*. [53], for example, used TIR images to show that selective logging of tropical forests had very little impact on thermal buffering compared to primary

Box 4. Water and Wind

Plant canopies not only buffer temperature, but also precipitation, relative humidity, and **vapor pressure deficit** (VPD) – which is exponentially related to air temperature. VPD drives transpiration in plants, and growth and survival can be impeded when VPD is high (responses vary greatly among species and depend on water supply and leaf temperature). In a degraded tropical forest landscape, models of understorey VPD generated by interpolating sensor-network data with LiDAR imagery (see Figure 1 in main text) suggest that tropical tree regeneration will be severely affected by global warming because of the close link between temperature and VPD [13]. The effect of remotely sensed canopy structure and composition on below-canopy VPD and moisture availability warrants further research, for example to better understand how moisture influences air and topsoil temperatures, and vice versa [31,96].

Topographic features, such as slope angle, affect the lateral surface and subsurface water flow. Airborne LiDAR-derived maps of topographic wetness and ruggedness are thus suitable to analyze the fine-scale variation of soil moisture and air humidity [97,98]. Detailed ecosystem structure data also deliver input parameters to better account for the effects of wind on microclimate. Canopy surface roughness and vertical canopy structure, for instance, improve wind modeling in heterogeneous forests and offer promising opportunities to make more accurate predictions of the near-surface wind fields [99,100].

forests, suggesting that selectively logged tropical forests may play an important role in retaining species with temperature niches that are disappearing under climate change. In aquatic systems, TIR images provide a means for landscape-level mapping of cold water patches (thermal refuges) along rivers – an important habitat element for riverine salmonids in times of climate warming [54]. Such maps provide valuable information to guide conservation efforts. We currently know little about the extent to which canopy surface temperatures measured by TIR images are coupled to the temperatures prevailing in the layers beneath the canopy surface, for example in forest understoreys or at the soil surface, although this knowledge would be helpful for using TIR images to model and map microclimatic air temperature. The difference between canopy leaf temperatures and ambient air temperatures can be highly variable and depends on canopy structure and species-specific leaf traits, such as aerodynamic leaf boundary-layer resistance and associated levels of atmospheric coupling [55]. Such analysis will also be subject to effects deriving from the ability of plants to regulate leaf temperature [50]. Research into the relationship between below-canopy temperatures measured by sensor networks (Box 3) and canopy temperature measured by TIR images will be necessary to further understanding of these linkages.

TIR radiation flux is affected by several factors in addition to leaf temperature, including the relative humidity, ambient temperature, wavelength-dependency of the emissivity and range of the camera, wind speed, and shadows [56]. Accurate surface temperature assessments using TIR imagery can thus be challenging. A key point is the emissivity, which is the ability of the surface of an object to emit thermal radiation [49,57]. The mean emissivity of surfaces from plants, soil, and rocks are in the range 0.903–0.997, and deriving surface temperature data from TIR images is thus complicated by the fact that not all surfaces in the image have similar thermal emissivity [57]. Furthermore, the spatiotemporal resolution of TIR imagery needs to be considered. Representing the climate conditions at a site requires TIR images taken across the full range of weather conditions, at day and night, and across seasons [2]. Although this may be feasible for terrestrial and potentially airborne TIR imagery, the high spatiotemporal resolution of such datasets comes at the cost of limited spatial coverage. Satellite TIR imagery provides surface temperature data with global coverage, although at too coarse a resolution to directly quantify microclimate (Figure 2). Even so, satellite TIR images can improve interpolations of temperature data from weather stations in areas with low station density [58]. Despite these challenges and limitations, the potential of TIR imagery in fundamental and applied microclimate ecology is substantial and should be explored in more detail.

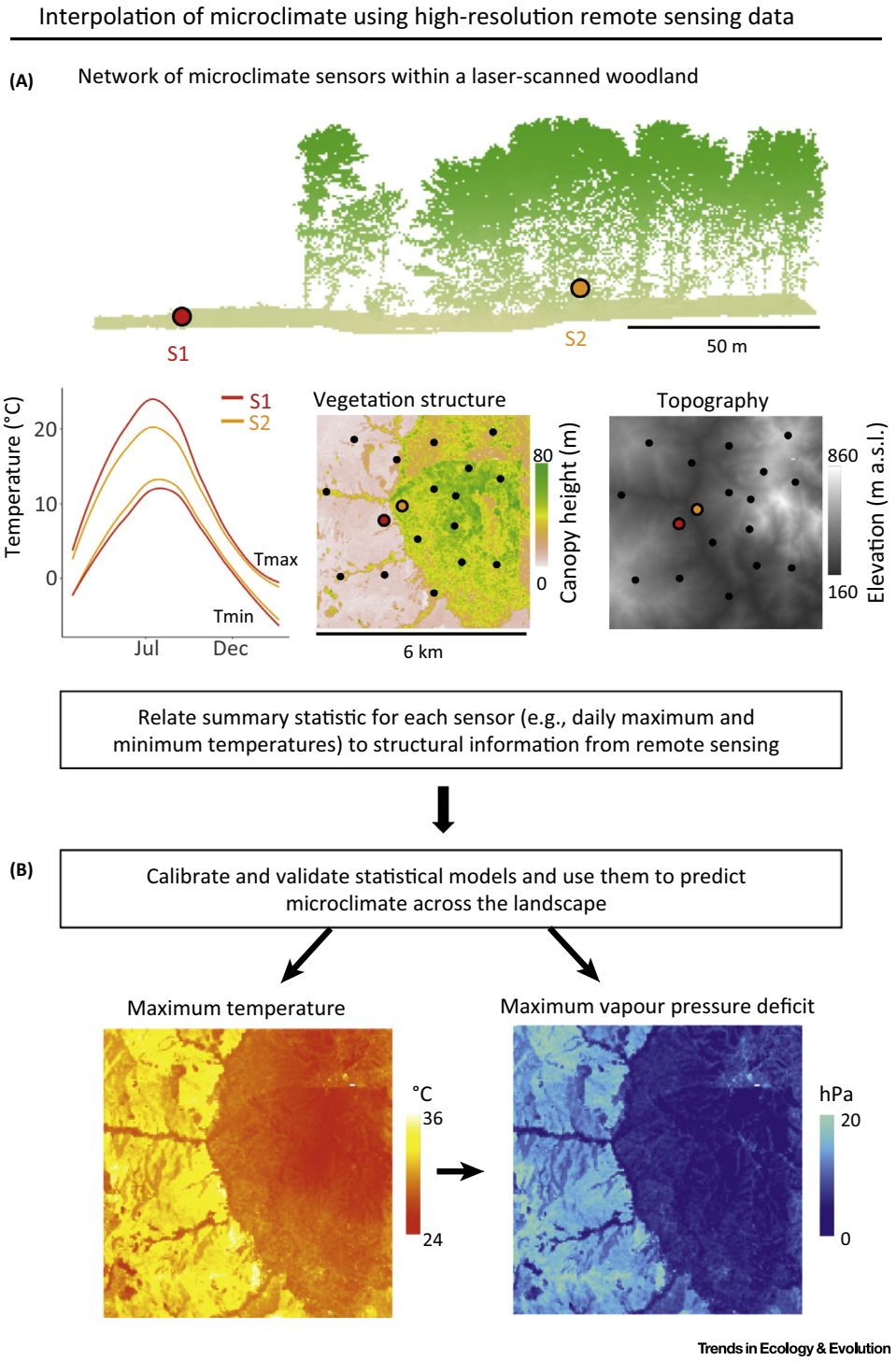

Figure 1. Conceptual Overview of the Approach Used To Generate Microclimate Maps from a Sensor Network. (A) Microclimate data are recorded using a network of sensors measuring air/soil temperature and humidity conditions, for example placed in the open (S1) and below tree canopies (S2), as shown by 3D airborne light detection and ranging (LiDAR) data in the top panel. The microclimate data from each sensor (S1, S2, and black dots) are then summarized in ecologically meaningful ways, for example to daily minimum (Tmin) and maximum (Tmax) temperatures, as shown in the middle

(See figure legend on the bottom of the next page.)

Another approach to microclimate mapping is to downscale macroclimate data obtained from macroclimatic grids [2,24], such as WorldClim 2 [58] and CHELSA [59], which are published at relatively coarse scales (typically 30″ resolution, equivalent to 1 km^2 at the equator). High-resolution remote sensing products, such as **digital terrain models** (DTMs), **canopy height models** (CHMs), and detailed ground and canopy albedo measurements, are used to generate indices of microclimatic processes related to solar radiation, **cold air drainage**, or topographic wetness from the grid data, and these indices are then related statistically to macroclimatic variables using regression [60–62]. Software such as R-packages implementing these approaches using freely available input data are now becoming available [14]. Because these models are based on macroclimate data that are available at a high temporal resolution, such models allow predictions of how microclimate conditions vary in time, thus tackling a key limitation of temporally limited approaches based on microclimate measurements from sensor networks (*cf* Box 3).

Mechanistic models may also use predictor variables derived from remote sensing data, but are fundamentally different in that they model heat and mass exchange between organisms and their environments, relying on functional relationships derived from the physical processes involved in creating microclimate [63,64]. Perhaps the most advanced mechanistic model is Niche Mapper™ [63], which downscales air temperatures based on a set of abiotic variables such as soil characteristics and macroclimatic meteorological variables including cloud cover, air temperatures, wind speeds, and shading. The model has been parameterized to predict lizard distributions in open habitats in Australia and the USA but does not currently include detailed modulating influences of plant canopies among its input variables [28,63].

Implications and Avenues for Microclimate Ecology

Ecologists are starting to appreciate the ways in which microclimate mapping technologies could improve their science. Correlative species distribution modeling (SDM) is often criticized for its reliance on coarse climate information [24] and its failure to incorporate physiological knowledge [8]. Using detailed spatiotemporal microclimate data in such models will allow more organism-centered approaches to determine species range boundaries and their climate change-related dynamics. This especially applies at the temperature-driven leading and trailing edges, where the response of organisms may be particularly susceptible to the availability of suitable microclimate and associated microrefugia [8,24,26,65,66]. Incorporating microclimate layers into SDMs thus holds large potential, but is still in its infancy. Using simulations, and focusing on maximum temperature of the warmest month, Lenoir *et al*. [24] found that using airborne LiDAR-derived variables to model microclimate decreases the extirpation risk of a virtual plant species under climate change compared to predictions based on downscaled climate data at coarser resolutions (Box 1). Such modeling results are physiologically more meaningful because they derive from comparison of the temperature niche of a species with realistic temperature dynamics driven by vegetation shading and cold air drainage.

Microclimate data will also help to shed new light into microclimatic effects on phenology – potentially quantified by remotely sensed vegetation indices such as the normalized difference

left panel, and related to vegetation structure and the topography mapped using remote sensing technologies (e.g., LiDAR), as shown for canopy height and elevation across a landscape in the tropical lowlands [13]. Abbreviation: m a.s.l, meters above sea level. (B) Statistical models are then used to predict microclimate across the entire mapped landscape and over time. In this example, maximum canopy height and topographic position were strong predictors of maximum daily air temperatures in the understorey (left), which explained small-scale variation of maximum vapor pressure deficit (VPD) (right), as indicated by the black arrows. Image adapted, with permission, from Jucker *et al*. [13].

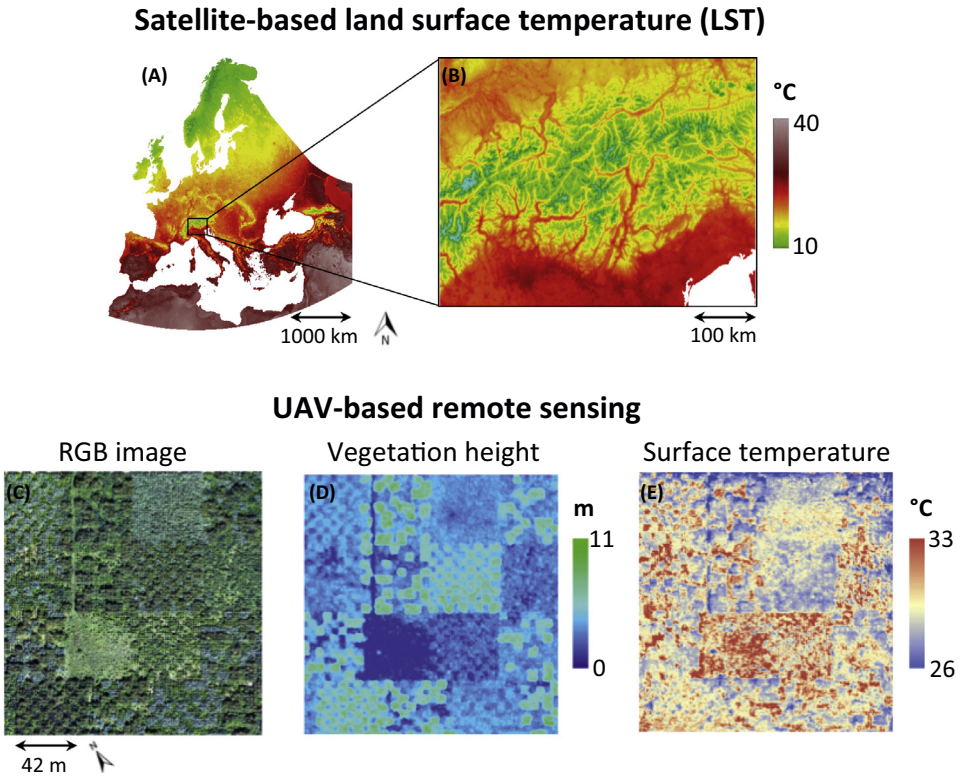

Figure 2. Thermal Infrared (TIR) Imaging Reveals Spatially Detailed Information about Surface Temperatures. Images (A) and (B) show land surface temperatures (LSTs) for Europe (EuroLST) derived from freely available MODIS satellite images with a pixel size of 250 m [84]. Data for images (C–E) were recorded at sub-meter resolution by an unmanned aerial vehicle (UAV) flown at 70 m height above ground during an exceptional drought in June 2017 in a tree diversity experiment in Belgium (www.treedivbelgium.ugent.be). Panel (C) is conventional red/green/blue (RGB) photography, panel (D) shows the vegetation height (m) determined by structure-from-motion analysis of overlapping photos, and panel (E) shows the surface temperature derived from the TIR image. We see that surface temperatures of plants on the ground are considerably higher than those of tree surfaces owing to different transpiration rates as a response to water shortage. The data were processed following Maes *et al*. [42].

vegetation index (NDVI) – and how these effects affect species distributions and species interactions. For instance, plant species-range limits may be driven by temperature extremes during key stages of phenology, such as extreme cold during bud-break of broad-leaved tree species [67]. Such extreme events are not represented in currently available climate data with coarse spatiotemporal resolution. Using remote sensing data to derive climate data at resolutions similar to those at which organisms perceive and respond to climate conditions is thus a timely task and will pave the way for more reliable predictions of species-range dynamics in response to climate change [27].

Microclimate mapping could also refine our understanding of species diversity patterns. Following the environmental heterogeneity hypothesis, microclimate heterogeneity is expected to be positively related to species richness (**alpha diversity**) [68], but this remains understudied. Similarly, investigating how spatial and/or temporal changes in microclimate contribute to **beta diversity** through environmental filtering deserves more attention [68,69]. For example,

a recent study found that microclimate on cooler, north-facing slopes affected plant community responses to climate change by delaying extinctions of species with low-temperature requirements [70]. Increased short-distance microclimatic variation is expected to affect the climatic debt in bird assemblages, for example by lowering the risk of population decline owing to the ability to avoid harmful climatic variation or by increasing landscape permeability which facilitates spatial tracking of climate change [71]. Spatiotemporal mapping of microclimate will thus be crucial to understanding how local phenomena give rise to large-scale processes. Estimating connectivity among fragmented habitats to evaluate the functionality of ecological networks, for instance, depends on reliable landscape-level representations of microrefugia, stepping stones, 3D habitat structure, and associated microclimate (e.g., ecological corridors such as hedgerows) because these attributes are crucial for species migration and gene flow [65,66,72].

The potential of remote sensing technologies to better understand and model microclimate is already recognized implicitly in the ecological literature. The widespread use of LiDAR to model species occurrence from habitat structure, for instance, relies implicitly on the assumption that LiDAR data can be used to assess microclimate conditions that are, at least partially, responsible for the fitness and distribution of an organism [73–75]. What is missing in such indirect approaches is how the measured environmental features actually drive and interact with the microclimate variables that are physiologically relevant to the species or the biological phenomena of interest, for example the minimum and maximum air temperatures relevant to the temperature tolerance of an organism [7]. In forests, our mechanistic understanding of how canopy structure and composition drive and interact with vertical radiation and temperature regimes to determine species habitat preferences and vertical niche partitioning is still incomplete. Indeed, the steep vertical microclimatic gradients within forests are increasingly appreciated for structuring arboreal biodiversity, particularly in the tropics [76–78], and the remote sensing approaches described here play a key role in filling this knowledge gap.

Microclimatic changes arising from forest management have been shown to exert strong controls on local plant communities and their response to macroclimate warming [21]. Thus, mapping of microclimate has far-reaching implications for conservation and other fields, such as forestry and agriculture [35]. Successful tree regeneration – planted or natural – strongly depends on microclimate conditions [12,60]. Maps of thermal and light regimes below different canopy conditions or in clear-cuts can help managers to optimize planting in accordance to tree species-specific temperature and light adaptations [12]. Similarly, microclimate maps would be helpful for managing agroforestry systems, such as those associated with coffee and cacao, where microclimates affect yield and the susceptibility to climate extremes [79]. In agriculture, precision farming of specialty crops increasingly relies on remote sensing technologies capturing the spatiotemporal variability of the microenvironmental conditions [80,81]. Mapping the thermal heterogeneity across landscapes improves the analysis and management of crop water status [52,80] and of how microclimate affects the occurrence and dynamics of pests [49,82].

Current Limitations and Future Directions

Field measurements of microclimate recorded with sensor networks are crucial for the development of landscape-scale maps, but sensor and sampling designs vary greatly between studies, making it difficult to synthesize results [2]. The need for standardized sampling approaches, centered around the following principles, is increasingly recognized: (i) field surveys are designed to represent the entire spatial and temporal gradients of the microclimate conditions in the study system, (ii) the timespan between the collection of field and remote

sensing datasets is short enough to prevent significant discrepancies, and (iii) measurement sites are precisely georeferenced using a differential global positioning system, such that the data can be spatially coregistered with the imagery. Simulations show that registration errors as small as 1 m when working with 10 m radius plots can create major uncertainty in forest properties estimated from airborne LiDAR [83]. Thus, also precisely locating species records, particularly of less-mobile species, is a prerequisite for sound inference about species–microclimate relationships.

The presented airborne remote sensing tools and data (i.e., involving airborne LiDAR and/or SfM) to map the effects of vegetation structure on microclimate near the ground work best in tall habitats such as forests, wood- and shrublands. In short-stature vegetation, such as grassland, heath, or crops, the level of structural detail picked up by airborne LiDAR and SfM may not be high enough to capture microclimate variation resulting from fine-scale differences in vegetation structure, but this remains to be tested. High-resolution TIR, however, provides the means to measure surface temperatures in both tall- and short-stature vegetation, but does not provide structural information necessary to interpolate microclimate measurements from sensor networks.

There is a pressing need to gather georeferenced microclimate data from different types of habitat across the globe, and a global archive and data portal facilitating data access would significantly promote progress in microclimate ecology. To complement temporal dynamics of microclimate data gained from downscaled macroclimate we need long-term microclimate data series [24]. This will enable an improved understanding of the drivers of microclimate dynamics and how they deviate from the macroclimate, which will have important implications for estimating the velocity, and thus impact, of climate change.

Many of the remote sensing approaches described here rely on data whose spatial coverage is growing but does not yet expand over continental and global scales. In the future, remedial satellite LiDAR data experiments, for example the Global Ecosystem Dynamics Investigation LiDAR (GEDI) or the ICESat-2 satellite project, may provide new avenues for analyzing and monitoring microclimate variation at larger temporal and spatial scales. Satellite missions employing synthetic aperture radar (SAR) systems, such as the launched TanDEM-X and planned Tandem-L missions, provide worldwide, repeated, and spatially detailed data for digital terrain elevation and forest height modeling. Incorporating these data into microclimate models may play a key role in increasing their spatial and temporal cover, and is expected to facilitate tracking of microclimatic changes in habitats with dynamic structural attributes, such as forest vegetation structure.

Concluding Remarks

We have shown that advances in remote sensing technologies are making it possible to map microclimate at fine spatiotemporal resolution and over large areas for the first time. This offers new opportunities to scale-up ecological knowledge about the organism–environment interactions at fine scales, promoting our understanding of species and ecosystem responses to environmental changes over broad scales.

Topographically controlled microclimate gradients have historically been studied in more detail than those controlled by 3D vegetation structure. LiDAR and photogrammetry provide key structural data to fill this gap, which is crucial given the contribution that vegetation structure makes to biodiversity. However, methodological efforts taking an ecological perspective in approximating microclimate via remote sensing tools will be necessary to make most out of the

Outstanding Questions

Improved, open-access, and easy-to-use methods based on remotely sensed canopy structure and composition for modeling and predicting microclimate in forests are needed. Such methods are necessary to further our understanding of light, temperature, and relative humidity regimes, and how these affect species behavior, performance, and distribution. Emphasis should also be given to quantifying the effect of local wind dynamics on microclimate.

How will microclimatic conditions change in response to climate warming? This will depend on the extent to which vegetation structure and topography modulate air temperature, and how changes in vegetation structure change solar radiation and wind regimes.

How does horizontal and vertical microclimate variation affect alpha- and beta-diversity?

What is the influence of microclimate buffering on species-range dynamics, biodiversity, and the climatic debt of species and communities?

How are microclimate gradients related to plant functional traits derived from hyperspectral imaging?

How can landscape-level mapping of microclimate contribute to our understanding of habitat connectivity and the functionality of ecological networks?

How are below canopy and soil microclimate linked to vegetation surface temperatures measured by thermal infrared (TIR) imagery?

How important is microclimate for driving phenological responses to climate change, and what are the implications thereof for species interactions and distributions?

available data and resources. The technological advances in remote sensing and the methodological advances in microclimate modeling call for coordinated efforts between remote sensing experts, climatologists, and ecologists to improve our predictive abilities on the role of microclimate in biodiversity and global change ecology.

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